

## Original Articles

## Calcification of coral assemblages in the eastern Pacific: Reshuffling calcification scenarios under climate change



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## ABSTRACT

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The rearrangement of coral assemblages may produce significant changes in coral community calcification, yet it is not understood how the modification of community structure in depauperate areas under climate change scenarios may affect reef functionality. Observed coral community calcification (OCC) was calculated using coral cover data from 126 sites across the eastern tropical Pacific (ETP). To assess the effect that species assemblages exert on potential coral community calcification (PCC) of ETP reefs, we implemented a novel permutation approach for this purpose. We contrasted OCC across the ETP against the PCC of hypothetical monospecific and maximum ecological evenness (ME) ETP reefs and monogenetic Indo-Pacific (IP) and Caribbean (C) reefs. Average coral cover ( $21 \pm 23\%$ ; mean  $\pm$  SD) and OCC ( $8.23 \pm 11.32 \text{ kg m}^{-2} \text{ yr}^{-1}$ ; mean  $\pm$  SD) in the ETP were not related to species richness but to *Pocillopora* abundance and calcification. For any level of coral abundance or species richness, the permutation model indicates that PCC depends on community structure: the PCC of *Pocillopora* monospecific reefs reaches its maximum; PCC drops to half of its potential when ME is attained; and PCC reaches its minimum when slow-growing species turn dominant. A dynamic model with changing community structure based on the differential species tolerance to climate change showed a similar pattern as the permutation model. ETP *Pocillopora* reefs have lower PCC than IP *Acropora*, IP *Pocillopora* and C *Acropora*. Massive taxa are more tolerant to climate change and could replace branching taxa if environmental pressure trends in the ETP continue, meaning an  $\sim 85\%$  drop in PCC.

## 1. Introduction

Coral reefs develop thanks to the ability of scleractinian coral to deposit calcium carbonate to build their skeletons and form complex three-dimensional structures as part of their growth (Carricart-Ganivet et al., 2012; Norzagaray-López et al., 2015). Coral calcification studies (per species, populations or community level) are used to assess the overall resilience, health state, fitness, and ecological success of corals and coral reefs at different spatio-temporal scales (Vecsei, 2004; Calderon-Aguilera et al., 2007; Manzello et al., 2008).

Reef-forming coral assemblages result from the combination of

physiological processes and the thresholds to environmental conditions of each coral species (Sheppard et al., 2009). Every coral species has an ecological functional role in the reef ecosystem (e.g., reef-building capacity, substrate complexity formation, carbonate stocks, tide or water flow protection), which may be redundant or shared by one or more species (Veron 2000; Hughes et al., 2018; McWilliam et al., 2018). Theoretically, coral species composition and community structure determine the benthic substrate architecture, habitat complexity, and coral community calcification of the coral reef ecosystem (Sheppard et al., 2009). Branching fast-growing coral are the main source of carbonates on most reefs around the world; they provide considerable

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habitat complexity for diverse organisms; however, they are more susceptible to environmental disturbance (Darling et al. 2013; Perry et al., 2015; Pratchett et al., 2015; Hughes et al., 2018). On the other hand, slow-growing massive coral have life-history strategies to resist and cope with environmental disturbance, but their growth morphologies provide a lesser degree of habitat complexity (Polunin and Roberts, 1993; Carreiro-Silva and McClanahan, 2012; Carricart-Ganivet et al., 2012).

A rearrangement of the coral assemblage in coral reefs (due to a changing environment for example), may produce significant changes in the coral community calcification (Wellington, 1982; Walther et al., 2002), due to the loss of key-species or functional entities since coral populations have different degrees of resistance and respond differentially to environmental pressures (Glynn et al., 2001; Loya et al., 2014; Pandolfi and Jackson, 2006; Pandolfi et al., 2011). A determining factor regarding this issue is whether the patterns of coral community assemblages (i.e., ecological dominance and evenness, species similarity) are equally successful in maintaining reef structural integrity under various species assemblage scenarios. An increase or drop in coral community calcification is not necessarily the only answer as populations of coral species remaining after a hypothetical reshuffling could maintain the net positive calcification production of a coral community (Hughes et al., 2012).

Considering that climate change is the major driver for the decline of coral community calcification in coral reefs (Kennedy et al., 2013); Alvarez-Filip et al. (2013) modeled the effect that different coral species assemblages and dominance shifts have on overall community calcification and reef rugosity, concluding that the loss and subsequent substitution of key reef-building genera by other opportunistic species with reduced ability to produce and maintain reef framework may compromise reef structural integrity and ecosystem functionality. Alvarez-Filip et al. (2013) propose that highly diverse coral communities (i.e. Indo-Pacific), may retain a certain degree of functionality under a hastily changing environment due to inherent species ecological functional redundancy; in contrast, in less-diverse ecosystems (in terms of coral species), like the Caribbean, coral assemblages may easily be dominated by coral species with a reduced capacity to produce and maintain reef framework (Aronson et al., 2002; Green et al., 2008; Alvarez-Filip et al., 2011; McWilliam et al., 2018). The authors highlighted the need to fully understand how modifying coral community structure in regions with different coral assemblage arrays may affect reef functionality.

In accordance with the hypothesis established by Alvarez-Filip et al. (2013), the scenario for the coral reefs of the eastern tropical Pacific Ocean (ETP) is not very encouraging. Coral reefs of the ETP have low coral species richness and coral community calcification compared to both the Caribbean and Indo-Pacific reefs (Manzello et al., 2017; McWilliam et al., 2018), due to the influence of environmental conditions (believed to limit or inhibit coral growth), such as fluctuations in sea temperature, seasonal upwelling events, El Niño/La Niña, low and variable pH, nutrient pulses and increased sedimentation (Manzello et al., 2008; Manzello, 2010a,b).

In the ETP region, coral reefs are mostly constructed by near-monogeneric communities of branching *Pocillopora* and massive *Porites* or *Pavona* (Guzmán and Cortés 1989a,b; Macintyre et al., 1993). Most of the reefs throughout the ETP share a typical zonation pattern: the shallow zone is dominated by *Pocillopora* spp., while massive species dominance increases with depth (Glynn et al., 2017). Although coral diversity increases in the deeper reef zones, coral cover and calcification declines and is minimal in the deepest zones; therefore, coral species assemblages in the ETP strongly rely on reef architecture and environmental factors (Glynn and Ault, 2000). Given that coral reefs in the ETP have low coral species richness, they are expected to have low ecological functional species redundancy; thus, a shift in coral species dominance driven by environmental variability as previously reported (Manzello et al. 2008; Manzello 2010b) may cause coral community

calcification, structural integrity, and overall reef functionality to drop.

The study aims to address the overall dependence of the coral community calcification to changes in coral community structure and composition, but not to quantify or describe detailed  $\text{CaCO}_3$  budgets along the ETP. By using coral community calcification estimates for 126 coral reefs across the ETP, from the Gulf of California to Panama, a novel permutation model and theoretical modeled reefs, we evaluated the effect that coral community structure and composition has on the coral community calcification of ETP coral reefs. Also, we used a dynamic model with changing community structure based on the differential species tolerance to climate change to make predictions about the potential coral community calcification (PCC) of the ETP reefs. Finally, our findings in the ETP are contrasted against hypothetical Indo-Pacific (IP) and Caribbean (C) coral assemblages to envision a worldwide coral carbonate production scenario.

## 2. Materials and methods

### 2.1. Coral cover data

Datasets of per species coral cover of 126 reef sites across the ETP, from the Gulf of California to Panama (Table S1), were compiled. Data were gathered from different sources. Overall, coral communities and reefs were surveyed using 25-m-long point-intersect transects, and data were recorded every 25 cm. Additionally, we searched the online sources ISI Web of Science, Google Scholar and other relevant databases for peer-reviewed literature. Finally, we directly contacted scientists asking for any available data pertaining to their study sites. Since coral cover per species were addressed using a variety of methods that differ in the scale of measurement, degree of subjectivity, and sample size, we standardized data to coral cover  $\text{m}^{-2}$ .

### 2.2. Analyses

Previously published (Wellington, 1982; Guzmán and Cortés 1989a,b; Glynn et al., 1996; Eakin, 1996; Maté, 1997; Jiménez and Cortés, 2003; Manzello, 2010b; Cabral-Tena et al., 2013; Norzagaray-López et al., 2015; Medellín-Maldonado et al., 2016; Norzagaray-López et al., 2017; Tortolero-Langarica et al., 2016, 2017a,b) annual extension rates ( $\text{cm yr}^{-1}$ ) and mean skeletal density ( $\text{g cm}^{-3}$ ) of each species as close and comparable as possible to each reef site in the ETP was used to calculate the observed coral community calcification OCC ( $\text{kg CaCO}_3 \text{ m}^{-2} \text{ yr}^{-1}$ ). When data was not available to any species or site, the average of the closest published growth and density data for each coral genus was used (Table S2).

Massive colonies were considered dome-shaped with similar growth rates across their surface (Eq. (1)). Meanwhile, per species mean branch diameter (cm) and branch density ( $\text{branches m}^{-2}$ ) published data (Veron, 2000; Paz-García et al., 2015) were used for calcification rate calculations of *Pocillopora* spp. (Eq. (2)).

$$\text{OCC}_M = \sum_{i=0}^n (gr_i \times sd_i \times cc_i) / 10 \quad (1)$$

Where  $\text{OCC}_M$  is the observed  $\text{CaCO}_3$  production of the massive coral community ( $\text{kg CaCO}_3 \text{ m}^{-2} \text{ yr}^{-1}$ ),  $gr_i$  is the growth rate ( $\text{cm yr}^{-1}$ ) of the species  $i$ ,  $sd_i$  is the skeletal density ( $\text{g CaCO}_3 \text{ cm}^{-3}$ ) of the species  $i$  and  $cc_i$  is the cover of the species  $i$ , 10 was inserted in the model as an adjustment coefficient to set the units as  $\text{kg CaCO}_3 \text{ m}^{-2} \text{ yr}^{-1}$  (Hubbard et al., 1990; Perry et al., 2012; Alvarez-Filip et al., 2013; Mallela, 2013).

$$\text{OCC}_B = \sum_{i=0}^n (((bdia_i \times (gr_i \times sd_i)) \times bden_i) / 1000) \times cc_i \quad (2)$$

Where  $\text{OCC}_B$  is the observed  $\text{CaCO}_3$  production of the branching coral community ( $\text{kg CaCO}_3 \text{ m}^{-2} \text{ yr}^{-1}$ ),  $bdia_i$  is the mean branch diameter (cm) of species  $i$ ,  $gr_i$  is the growth rate ( $\text{cm yr}^{-1}$ ) of the species  $i$ ,  $sd_i$  is the skeletal density ( $\text{g CaCO}_3 \text{ cm}^{-3}$ ) of the species  $i$ ,  $bden_i$  is the mean branch density ( $\text{branches m}^{-2}$ ) and  $cc_i$  is the cover of the species  $i$

(Hubbard et al., 1990; Perry et al., 2012; Alvarez-Filip et al., 2013; Mallela, 2013).

Due to the lack of site-specific variables such as erosion (biological, physical or chemical), individual coral colony geometric proportions and size, and overall reef rugosity for addressing detailed carbonate budgets as suggested by Perry et al. (2012) for each of the 126 sites across the ETP, it is assumed OCC solely as the sum of Eqs. (1) and (2). By removing site-specific variables from calculations, it is acknowledged that calcification estimates may, to some extent, be biased (over or underestimated), nevertheless it can confidently be used to test the effect that coral community structure and composition has on the coral community calcification of ETP coral reefs.

To assess the effect that coral assemblage excerpts on the hypothetical potential coral community calcification (PCC) of coral reefs in the ETP, first, we modeled changes in the relative abundance of seven of the most widespread and relevant reef forming species in the studied area (*Pocillopora damicornis*, *Pocillopora verrucosa*, *Pocillopora capitata*, *Porites panamensis*, *Porites lobata*, *Psammocora stellata*, *Pavona gigantea*, Glynn et al. 2017). Through a novel permutation approach, each model (1716 possible combinations) was built in such a way that the sum of all relative abundances reached the current average coral cover of the ETP calculated with our compiled data (21%).

Second, we compared the OCC across the ETP against two sets of hypothetical models: (1) PCC of monospecific reefs (i.e., each of the reef sites was dominated by only one coral species), (2) PCC as if reefs had reached its maximum ecological evenness (i.e., each species contributes with the same relative abundance).

Third, to make predictions about the PCC of the ETP reefs under steady climate change pressure, we constructed a dynamic model similar to the proposed by Alvarez-Filip et al. (2013). Community structure changes were based on the differential species tolerance to the combination of thermal stress and ocean acidification, i.e. more tolerance from massive and sub-massive species (*P. gigantea*, *P. lobata*, *P. panamensis* and *P. stellata*) in comparison to branching species (*P. damicornis*, *P. verrucosa* and *P. capitata*) (Manzello, 2010b; Manzello et al., 2017) and expected drops (approx. 1% per year) on coral growth rates in the ETP (Manzello, 2010b). In this model a hypothetical coral community with the presence of seven-species was simulated; in the simulation, the starting community structure was built in a hierarchical (calcification rate) manner. We simulated a steady loss of *Pocillopora* spp. cover over time (1% per year) and a hierarchical (calcification rate) reciprocal increase in the abundances of massive and sub-massive species, but also resembling the coral species dominance turnover documented after massive coral mortality events in the ETP (Guzman and Cortés 2007; Glynn et al. 2009; Glynn et al. 2017). The model was stopped when all pocilloporid species had 0% cover in the community. Overall coral cover of the dynamic model remained constant through time (21%).

Fourth, to contrast and contextualize the PCC of the ETP with coral communities from the IP and C, we built hypothetical models using ETP, IP and C coral growth data. To build the model, coral cover of the 126 reef sites across the ETP was used as a template to generate PCC for nine hypothetical monogenetic coral communities (three for each region), as if each community was dominated by one coral genus. *Acropora*, *Pocillopora*, *Orbicella*, *Pavona* and *Porites* were selected because of their reef-building importance, architectural relevance and commonness across regions (Alvarez-Filip et al. 2013; Glynn et al. 2017). Coral growth data for IP and C were obtained from the Reef-Budget Project database (<http://geography.exeter.ac.uk/reefbudget/>) and averaged by genus in each area.

### 2.3. Statistical analyses

To test the dependency of overall coral cover and OCC to the observed species richness and per species coral cover and calcification, datasets were fitted through forward stepwise multiple linear regression

**Table 1**

Multiple linear regression models between per species coral cover and calcification vs. overall coral cover and coral community calcification of ETP reefs. Bold numbers indicate more than 30% of explained variance

Species	Cover (N = 126)		Community calcification (N = 126)	
	R <sup>2</sup> = 0.86, P < 0.001	R <sup>2</sup> = 0.90, P < 0.001	Beta	P
<i>Porites panamensis</i>	0.18	< 0.001	0.02	< 0.001
<i>Porites lobata</i>	<b>0.32</b>	<b>&lt; 0.001</b>	0.05	< 0.001
<i>Pocillopora damicornis</i>	<b>0.57</b>	<b>&lt; 0.001</b>	<b>0.63</b>	<b>&lt; 0.001</b>
<i>Pocillopora verrucosa</i>	<b>0.40</b>	<b>&lt; 0.001</b>	<b>0.34</b>	<b>&lt; 0.001</b>
<i>Pocillopora capitata</i>	0.16	< 0.001	0.12	< 0.001
<i>Pocillopora meandrina</i>	0.08	< 0.001	0.09	< 0.001
<i>Pocillopora eydouxi</i>	0.11	< 0.001	<b>0.32</b>	<b>&lt; 0.001</b>
<i>Pocillopora inflata</i>	0.03	< 0.001	0.06	< 0.001
<i>Pocillopora effusa</i>	0.03	< 0.001	0.06	< 0.001
<i>Pavona gigantea</i>	0.08	< 0.001	0.03	< 0.001
<i>Pavona clavus</i>	0.05	< 0.001	0.05	< 0.001
<i>Pavona varians</i>	0.02	< 0.001	0.01	< 0.001
<i>Pavona duerdeni</i>	0.02	< 0.001	0.01	< 0.001
<i>Psammocora stellata</i>	0.06	< 0.001	0.04	< 0.001
<i>Psammocora superficialis</i>	0.05	< 0.001	0.01	< 0.001
Species richness	0	1	0	1

models. Finally, OCC and PCC of monospecific and monogenetic hypothetical reefs and observed coral cover (of each of the 126 ETP sites) were fitted through simple linear regression models after checking for normality and homogeneity of variances using Kolmogorov-Smirnov and Bartlett tests, respectively. To test if the slopes of the linear models (observed vs hypothetical monospecific ETP coral communities, hypothetical monogenetic ETP coral communities vs IP vs C) were different, a one-way analysis of covariance (ANCOVA) was used. Statistical analyses were performed with STATISTICA v7.0 software (StatSoft Inc., 2004) and PAST v3.06 software (Hammer et al., 2001).

## 3. Results

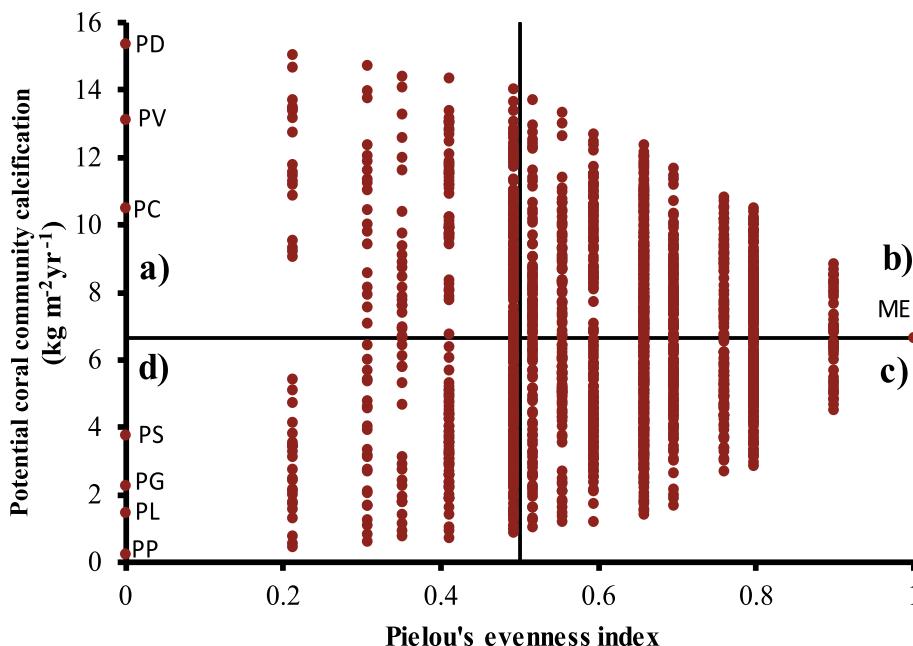
### 3.1. Coral cover and coral community calcification in the ETP

Coral cover across sites in the ETP ranged from 0.2% to 86% with an average of  $21 \pm 23.2\%$  (mean  $\pm$  SD). Multiple linear regression showed that overall coral cover depended on the coverage of all species ( $R^2 = 0.86$ ,  $n = 120$ ,  $P < 0.001$ ) (Table 1), but only *Pocillopora damicornis* (Beta = 0.57), *Pocillopora verrucosa* (Beta = 0.40), and *Porites lobata* (Beta = 0.32) accounted for more than 30% of the explained variance, suggesting that overall ETP coral cover is mainly explained by the abundance *Pocillopora damicornis* and *Pocillopora verrucosa* and to a lesser extent, by *Porites lobata* cover (Table 1). Meanwhile, observed species richness did not explain any of the model variance (Beta = 0).

According to our model, average brute observed coral community calcification (OCC) of reef sites in the ETP is  $8.22 \pm 11.32 \text{ kg m}^{-2} \text{ yr}^{-1}$  (mean  $\pm$  SD) but ranged from 0.02 to  $43.92 \text{ kg m}^{-2} \text{ yr}^{-1}$ . OCC depended on calcification from all species ( $R^2 = 0.90$ ,  $n = 120$ ,  $P < 0.001$ ), but only *Pocillopora damicornis* (Beta = 0.63), *Pocillopora verrucosa* (Beta = 0.34), and *Pocillopora eydouxi* (Beta = 0.32) accounted for more than 30% of the explained variance, meaning that *Pocillopora* spp. calcification greatly defines OCC of ETP coral reefs (Table 1). Additionally, observed species richness did not explain any of the OCC variance (Beta = 0).

### 3.2. Models

Changes in coral community calcification of ETP reefs depend on the coral species assemblage structure (Fig. 1). Although several scenarios arose from the model, they can be synthesized by a few



**Fig. 1.** Hypothetical potential coral community calcification (PCC) of ETP reefs when coral species assemblages structure is permuted. Each model (dot) was built in such a way that the sum of all relative species abundances reached 21% of overall coral cover. PD: *Pocillopora damicornis*, PV: *Pocillopora verrucosa*, PC: *Pocillopora capitata*, PP: *Porites panamensis*, PL: *Porites lobata*, PS, *Psammocora stellata*, PG: *Pavona gigantea*, ME: Maximum ecological evenness. a) PCC when coral cover is dominated by PD, PV or PC. b) PCC when PD, PV or PC dominance is shared with subordinate species, c) PCC when PP, PL PS, or PG dominance is shared with subordinate species, d) PCC when coral cover is dominated by PP, PL PS, or PG.

tendencies. First, when reefs are dominated by fast-growing species such as *Pocillopora damicornis*, *Pocillopora verrucosa* or *Pocillopora capitata*, hypothetical potential coral community calcification (PCC) is at, or near its maximum (Fig. 1a). Second, when pocilloporid dominance decreases and the coral cover is shared with slow-growing species, PCC drops (Fig. 1b) and reaches half of its potential when maximum ecological evenness in the community is attained. Third, PCC may continue to fall as slow-growing species (*Psammocora stellata*, *Pavona gigantea*, *Porites* spp.) become dominant in the community (Fig. 1c). Finally, PCC reaches its minimum when reefs are exclusively built by *Porites panamensis* or *Porites lobata* (Fig. 1d). We iteratively searched for the effect of species richness ( $> 3 < 15$  coral species) and coral cover ( $> 1\% < 95\%$  coral cover) in the proposed model. It is important to highlight that the permutation model shows the same general pattern irrespective of species richness, and overall coral cover (Fig. S1), hence it may confidently be employed under any species richness and coral cover combination scenario.

OCC of ETP reefs is highly variable among sites, still, there is an overall tendency ( $r^2 = 0.8$ ,  $n = 120$ ,  $P < 0.001$ ) to increase in sites with larger coral cover (Fig. 2). OCC is slightly lower than PCC of monospecific *Pocillopora* simulated reefs but higher than the PCC of sites with maximum ecological evenness or monospecific reefs constructed by slow-growing massive (*Porites panamensis*) or leafy species (*Pavona gigantea*). Concurrently, analysis of covariance indicates that OCC of ETP reefs is meaningfully reduced when compared with hypothetical monospecific *Pocillopora damicornis* reefs ( $F = 10.76$ ,  $P = 0.001$ ), but is indistinguishable from calcification of monospecific reefs constructed by *Pocillopora capitata* ( $F = 2.01$ ,  $P = 0.15$ ) and *Pocillopora verrucosa* ( $F = 1.76$ ,  $P = 0.18$ ). On the contrary, OCC is higher than the PCP accomplished by hypothetical sites with maximum ecological evenness or monospecific reefs constructed by *Psammocora stellata* ( $F = 211.7$ ,  $P < 0.001$ ), *Pavona gigantea* ( $F = 247.8$ ,  $P < 0.001$ ), *Porites lobata* ( $F = 190.8$ ,  $P < 0.001$ ), or *Porites panamensis* ( $F = 287.4$ ,  $P < 0.001$ ). In summary, OCC is near its maximum potential in ETP reefs.

The dynamic model (Fig. 3) shows the expected variations in community structure and the subsequent change of PCC of ETP reefs through time due to thermal stress and ocean acidification pressure but with constant overall coral community cover (21%). This model considers the constant decline in coral calcification rates observed in the *Pocillopora* corals of the ETP recently accounted by Manzello (2010b); if

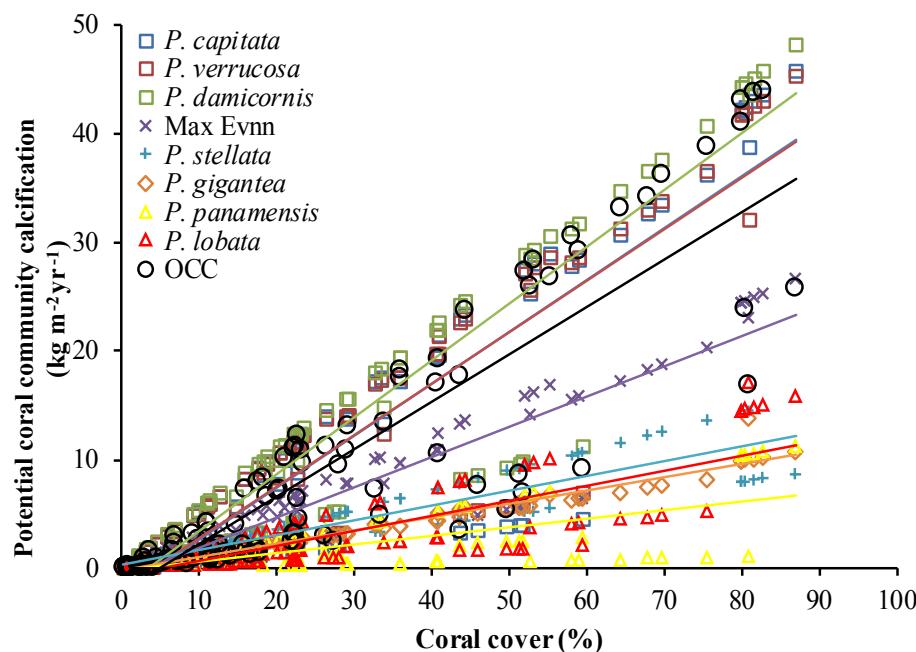
the overall community structure is not modified this would translate into a PCC drop of ~20%. However, if coral community structure begins to change as projected due to differential species sensitivity to thermal stress and ocean acidification pressure, PCC dramatically drops (~85%, initial vs. final community structure) as pocilloporid species cover drops and is replaced by massive species (*Pavona gigantea* and *Porites lobata* were dominant when the model stopped) in a very similar pattern as the one described by the permutation model (Fig. 1).

PCC of nine hypothetical monogeneric reefs was contrasted (Fig. 4). Overall, hypothetical reefs dominated by fast-growing branching genera (Fig. 4a) had higher PCC than those built by slow-growing massive or leafy genera (Fig. 4b). Regarding models derived from branching genera, *Acropora* spp. stands as the genus with largest PCC in comparison to the PCC of reefs constructed by *Pocillopora* spp. Also, PCC of IP acroporids is larger than the PCC of C ones; in the same way, PCC of IP pocilloporids is larger than the PCC of ETP pocilloporids. To summarize, the maximum PCC of ETP coral reefs is 62%, 53%, and 25% lower than the highest PCC of IP *Acropora*, C *Acropora*, and IP *Pocillopora*, respectively. Concerning hypothetical reefs of massive and leafy morphology, PCC of IP *Porites* was the highest, while PCC of C *Porites* was the lowest and the PCC of monogeneric C *Orbicella* and ETP *Pavona* are indistinguishable but lower than the observed in IP *Porites*. In all cases, ANCOVA results indicated differences among all simulated reef slopes ( $P < 0.05$ ), except between ETP *Pavona* and C *Orbicella*, which had similar slopes ( $P > 0.05$ ).

## 4. Discussion

### 4.1. Coral community structure, not species richness drives coral calcification in the ETP

The data presented in this study provide insights regarding the patterns of the coral community calcification across ETP coral reefs. Our results show evidence indicating that coral community calcification of ETP reefs does not depend on overall coral cover or observed species richness as previously suggested (Gardner et al., 2003; Mumby et al., 2007), instead, it strongly relies on the coral structure of the assemblage as reported in other areas (Alvarez-Filip et al., 2011, 2013; Perry et al., 2014; Januchowski-Hartley et al., 2017). Multiple regression analysis indicate that coral cover is not explained by the observed species richness (0% of explained variance), but mostly by

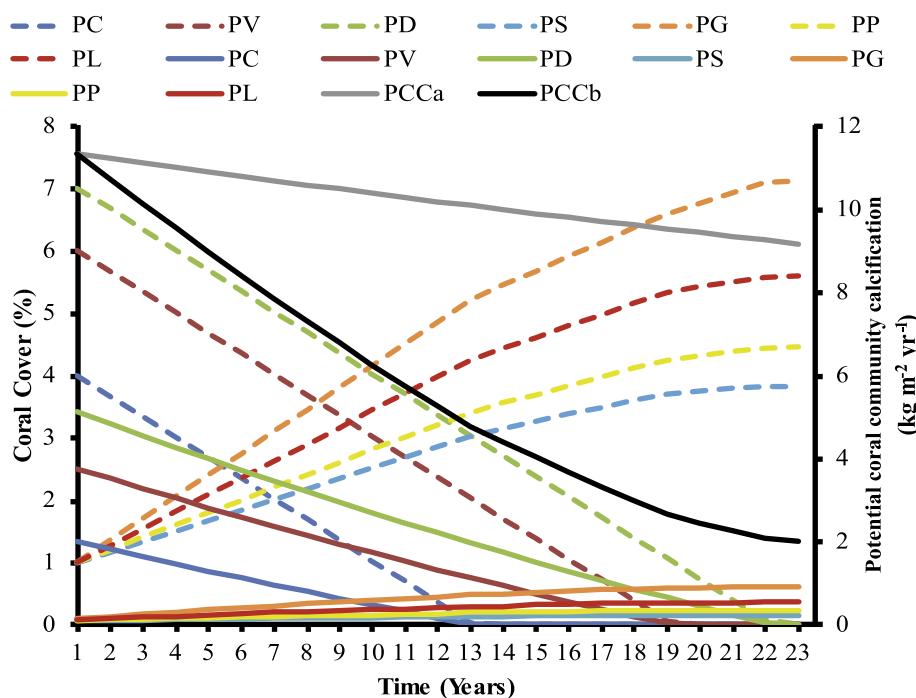


**Fig. 2.** Observed coral community calcification (OCC, open circles, black line) of ETP reefs and potential coral community calcification (PCC) of hypothetical reefs with maximum ecological (X purple line) evenness and monospecific reefs (squares *Pocillopora* species, triangles *Porites* species, rhombus *Pavona gigantea*, cross *Psammocora stellata*, each line color corresponds to its marker color).

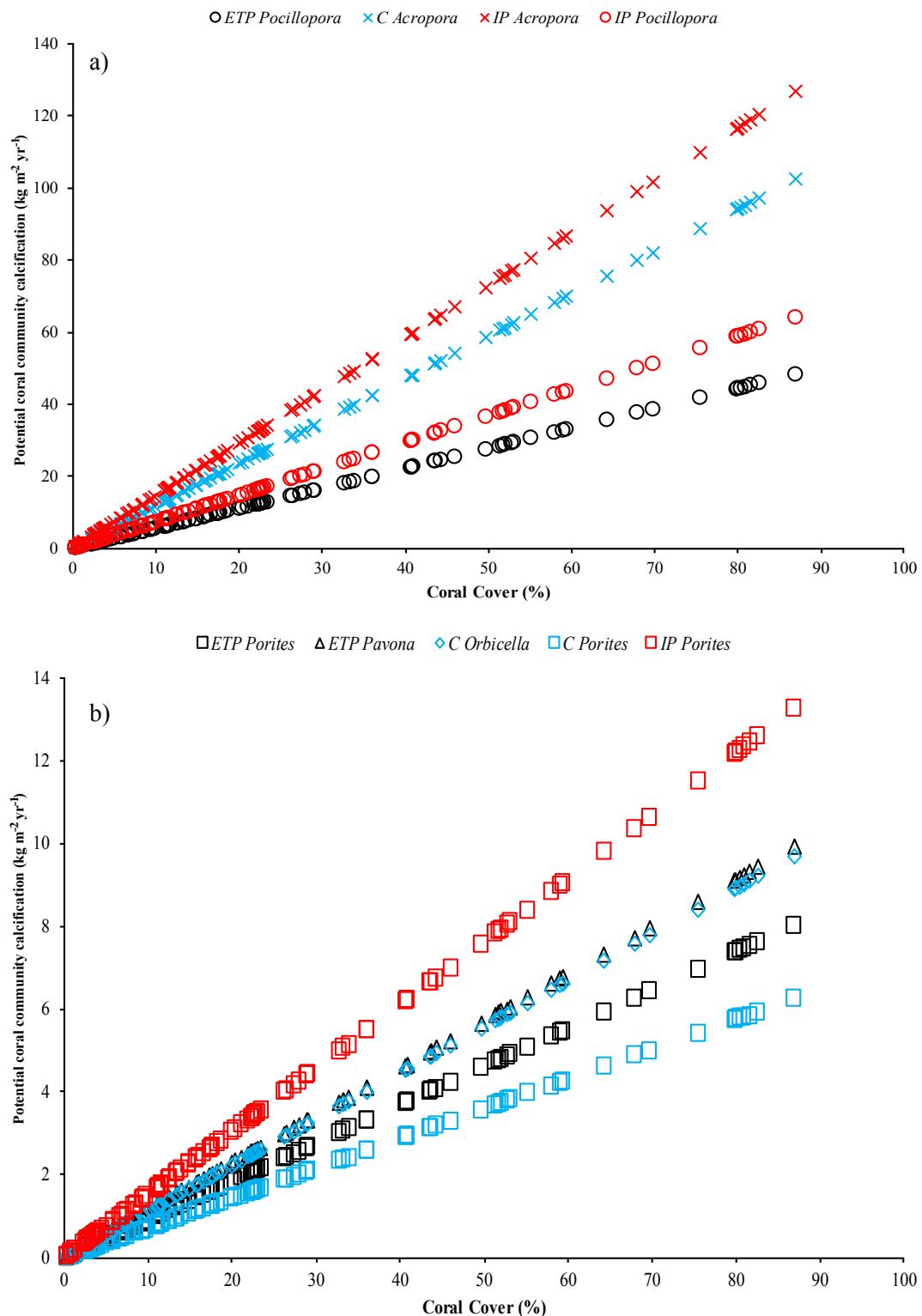
the coral coverage of a limited number of *Pocillopora* (75% of relative coral cover) species, especially *Pocillopora damicornis* and *Pocillopora verrucosa* (57% and 40% of the explained variance, respectively), and to a lesser extent, *Porites lobata* cover (32%), while *Porites spp.*, *Pavona spp.*, or *Psammocora spp.* contribute only marginally to overall coral cover. Also, regression analyses indicate that OCC across our studied reef sites was not explained by observed species richness (0% of explained variance), but mostly by the carbonate production of *Pocillopora* species, mainly *Pocillopora damicornis*, *Pocillopora verrucosa* and *Pocillopora eydouxi* (63%, 34%, and 32% of explained variance), species which also contributed the highest relative calcification rates in the area (Manzello, 2010b; Medellín-Maldonado et al. 2016; Tortolero-Langarica et al. 2017a). It is quite revealing that reef sites in the ETP with high coral coverage (> 30%, even > 80%, Fig. 2) have low OCC

because they are dominated by species other than *Pocillopora* spp. In summary, our data suggest that reef systems in the ETP can be functional (in terms of coral cover and OCC) regardless of species richness, if pocilloporids are the main reef builders in the area.

Our observations suggesting that carbonate production on the ETP relies on the scleractinian community assemblage are fully supported by the newly implemented permutation model (Fig. 1). The model unambiguously indicates that when fast-growing branching coral species (*Pocillopora* spp.) dominate the coral cover of ETP reefs, PCC reaches its maximum. PCC is at a minimum when reefs are dominated by massive coral species (mainly *Porites* spp.), and at half of its maximum when maximum ecological evenness is achieved. Interestingly, the permutation model shows that both the highest and lowest PCC occur when species richness is equal to one (ecological



**Fig. 3.** Changes in community structure (coral cover) and hypothetical potential coral community calcification (PCC) of a theoretical ETP reef through time under constant climate change pressure. Overall coral cover of the theoretical reef was set to 21%. PD: *Pocillopora damicornis*, PV: *Pocillopora verrucosa*, PC: *Pocillopora capitata*, PP: *Porites panamensis*, PL: *Porites lobata*, PS: *Psammocora stellata*, PG: *Pavona gigantea*, PCCA: PCC considering the effect of thermal stress and ocean acidification in calcification rates, PCCb: PCC considering the effect of thermal stress and ocean acidification in calcification rates and in coral community structure. Dashed lines represent coral cover, continuous lines represent PCC.



**Fig. 4.** Hypothetical potential coral community calcification (PCC) of simulated monogenetic reefs from the eastern tropical Pacific (ETP), Indo-Pacific (IP) and Caribbean (C). a) branching corals, b) massive/leafy corals. Dots, *Pocillopora*; X, *Acropora*; squares, *Porites*; triangles, *Pavona*; rhombus, *Orbicella*; black markers, ETP; red markers, IP; blue markers, C.

evenness = zero); in other words, PCC is disconnected from the number of coral species present in the community. Overall, the OCC of ETP reefs are located in the (a) and (b) quadrants of the permutation model, meaning that neither overall cover or species richness provide sufficient information to assess community calcification in the area, but species composition and the abundance of some species (*Pocillopora* spp.

contributes 91.56% of relative community calcification) play an important role in reef PCC and therefore, in overall health, stability and complexity of the ecosystem. In this regard, it is relevant that OCC of the ETP reefs is indistinguishable from the PCC of *P. verrucosa* and *P. capitata* monospecific reefs, meaning that OCC is currently functioning near its maximum potential in the ETP.

Our results highlight the importance of *Pocillopora* spp. on reef framework construction in the ETP. The relevance that *Pocillopora* spp. has in the ETP has been strongly documented (Glynn and Ault, 2000; Reyes-Bonilla, 2003; Glynn et al., 2017), as most coral reefs across the ETP are dominated by *Pocillopora* spp. as consequence of their rapid growth and high skeletal density which provides a competitive advantage over ecological and geological timescales (Glynn et al., 2017; López-Pérez, 2017), when compared with massive species that contribute to a lesser extent to the overall reef framework (Glynn and Ault, 2000; Reyes-Bonilla and López-Pérez, 2009). However, there are areas, such as the northern part of the Gulf of California (Reyes-Bonilla and López-Pérez, 2009), some reefs in the Revillagigedo Islands (Reyes-Bonilla et al., 1999), Clipperton Atoll (Glynn et al., 1996), and some sites in Central America (Guzmán and Cortés, 1993), in which massive corals are the major reef frame builders but displays sensibly reduced carbonate production.

In absence of erosion, the observed brute coral community calcification across reef sites in the ETP is  $8.22 \pm 11.32 \text{ kg m}^{-2} \text{ yr}^{-1}$  (mean  $\pm$  SD) and the brute PCC of a hypothetical ETP reef (21% coral cover average, shifting dominance of seven species) is  $5.61 \pm 1.86 \text{ kg m}^{-2} \text{ yr}^{-1}$  (mean  $\pm$  SD), but when coralline algae production ( $1.87 \text{ kg m}^{-2} \text{ yr}^{-1}$ ) and carbonate erosion ( $4.83 \text{ kg m}^{-2} \text{ yr}^{-1}$ ) are incorporated (Eakin 1992, 1996), average net contribution is  $5.27 \pm 8.35 \text{ kg m}^{-2} \text{ yr}^{-1}$  (mean  $\pm$  SD) and  $2.65 \pm 1.86 \text{ kg m}^{-2} \text{ yr}^{-1}$  (mean  $\pm$  SD) respectively. Such values are similar and in range with some observations in the ETP (Manzello et al., 2017) and comparable to low carbonate budgets in the Caribbean ( $\sim 2 \text{ kg m}^{-2} \text{ yr}^{-1}$ ; Perry et al. 2014), but below carbonate budgets from fore-reefs in the Indo-Pacific ( $5 \text{ kg m}^{-2} \text{ yr}^{-1}$ ; Montaggioni, 2005), the Caribbean ( $3.5 \text{ kg m}^{-2} \text{ yr}^{-1}$ ; Perry et al. 2013), the Seychelles ( $\sim 3.5 \text{ kg m}^{-2} \text{ yr}^{-1}$ ; Januchowski-Hartley et al. 2017), and Palau and Yap ( $13.1 \text{ kg m}^{-2} \text{ yr}^{-1}$ ;  $14.1 \text{ kg m}^{-2} \text{ yr}^{-1}$ ; van Woesik and Cacciapaglia, 2018). However, if we compare the calculated carbon budget from Cabo Pulmo, the northernmost coral reef in the ETP (Reyes-Bonilla et al. 1997; Glynn and Ault, 2000; Norzagaray-López et al. 2015), net PCP is  $3.48 \text{ kg m}^{-2} \text{ yr}^{-1}$ , which is similar to the observed in the Caribbean and the Seychelles. Yet, while the  $\text{CaCO}_3$  production of Cabo Pulmo is high, most of the reef-derived sediments are transported off-reef due to oceanographic conditions; hence, sedimentologically speaking, functions in a limited way like a coral reef (Riegl et al. 2007).

#### 4.2. Coral community calcification scenarios under a changing environment: Massive slow-growing winners vs. branching fast-growing losers

In accordance to our models, *Pocillopora* dominated reefs in the ETP calcify 666.38% ( $13.01 \pm 2.42 \text{ kg CaCO}_3 \text{ m}^{-2} \text{ yr}^{-1}$ ; mean  $\pm$  SD) more carbonates than reefs dominated by massive or leafy species ( $1.95 \pm 1.14 \text{ kg CaCO}_3 \text{ m}^{-2} \text{ yr}^{-1}$ ; mean  $\pm$  SD). These results are especially relevant given that coral species and populations in the ETP have shown contrasting mortality and resilience to environmental pressures (Pandolfi et al., 2011; Manzello et al., 2017), leading to differential reef deterioration trajectories, especially in the context of thermal stress and ocean acidification, which act as synergic stressors and are expected to drive the overall coral assemblage structure and dominance (winners vs. losers) patterns in a long-term scenario across the ETP (Glynn et al. 2001; Manzello, 2010a, 2010b; Manzello et al., 2017). There is evidence suggesting that pocilloporids have developed higher thermal stress tolerance and some ability to cope with warming stress in comparison with *Pavona*, which has been attributed to differential flexibility in hosting resistant endosymbionts (LaJeunesse et al., 2007; Manzello, 2010b; Baker et al., 2017). Nevertheless, corals harboring thermally tolerant endosymbionts have lower calcification rates when compared with species hosting temperature-sensitive symbionts (Little et al., 2004), so it would come down to a tradeoff between thermo-tolerant symbionts vs. reduced carbonate production.

Calcification of *P. damicornis* is positively related with aragonite saturation, while pavonid corals can maintain higher calcification rates in low aragonite saturation environments, hence massive corals may be more tolerant to acidification than the Pocilloporidae (Manzello, 2010b). Despite their endosymbiont sensitivity to thermal stress and their lower temperature bleaching thresholds, massive corals, thanks to their morphology, rarely experience complete mortality as tissues on the periphery of the colony not exposed to direct sunlight usually survive, thus making effective bleaching recovery a possibility (Glynn et al., 2001).

In summary, massive coral taxa appear to be more tolerant to the synergic effects of ocean acidification and warming (Hughes et al., 2018). It is possible that branching morphology corals (losers) will begin to diminish their coverage and be replaced by corals with massive morphology (winners), as seen in our dynamic community structure model (Fig. 3), if environmental pressure trends in the ETP continue (Manzello et al., 2017). The loss of coral cover of *Pocillopora* and its subsequent replacement by massive species, as previously documented in some areas of the ETP after massive mortality events (Guzman and Cortés, 2007; Glynn et al., 2009), would have a strong effect in reef framework complexity but also on the PCC which may experience a drop by one order of magnitude or more ( $\sim 85\%$  drop), depending of the overall coral cover of the remaining species. Whether these changes would have a long-term cascade effect or compromise reef functionality or stability of reef-associated biodiversity, as seen in the Caribbean reefs due to the extensive loss of acroporid species cover and its subsequent reef flattening (Alvarez-Filip et al., 2009), has yet to be determined.

#### 4.3. Worldwide coral community calcification context

The coral community calcification of monogenetic reefs (discarding erosion), varies largely among taxa and across regions (i.e., ETP, IP and C). When comparing branching fast-growing coral (highest potential source of carbonates in each area), IP *Acropora* has the uppermost calcification in comparison to any other reef-builder; on the contrary, ETP *Pocillopora* has the lowest calcification: As such, the highest PCC of ETP reefs is lower than any of the other largest carbonate producers worldwide. On the other hand, hypothetical coral communities of massive genera achieve maximum calcification when IP *Porites* are the main builders but show the lowest carbonate production with C *Porites*, while C *Orbicella* and ETP *Porites* will attain similar carbonate production. From the above hypothetical models, two possible scenarios arise. First, if coral cover in a community is dominated by branching species in all areas, reefs from the IP would have the highest PCC, followed by C and lastly by ETP reefs. Second, if branching coral decrease their coverage regarding their massive counterparts due to environmental pressures as predicted for all areas around the world (Alvarez-Filip et al., 2009; Pandolfi et al., 2011; Manzello et al., 2017; Hughes et al., 2018) the IP will continue to have the highest PCC followed by the ETP, leaving the C with the lowest PCC. The overall resilience and resistance of branching corals (regardless of the species), as suggested by the models (Alvarez-Filip et al., 2013; this study), will drive the future of PCC and habitat complexity of coral reefs globally. Once again, the models indicate that areas with higher ecological redundancy (higher branching species richness) would retain high PCC and habitat complexity. IP reefs, for example, hosts numerous *Acropora* and *Pocillopora* species. If by any environmental pressures some of these species are locally removed or even if a genus becomes completely extinguished but another one prevails, the reefs would retain considerable PCC and habitat complexity. However, the scenario for C and ETP reefs is critical since only a reduced number of fast-growing branching species of each genus (*Acropora palmata*, *Acropora cervicornis* and *Acropora prolifera* in C; *Pocillopora damicornis*, *Pocillopora verrucosa*, *Pocillopora capitata*, *Pocillopora meandrina*, *Pocillopora eydouxi*, *Pocillopora inflata*, and *Pocillopora effusa* in ETP) are present at each area; hence, the removal of a

species will result in a drastic drop in PCC and habitat complexity in both areas. Our models suggest that if a few fast-growing branching species remain in each area, near-maximum PCC and habitat complexity levels are achievable.

Regardless of which scenario proves to be accurate in the future, ETP reefs will have to overcome several challenges to ensure their resilience over time in a hastily changing environment. For example, despite large or small carbonate production and framework complexity, ETP reefs tend to be highly porous, uncemented accumulations of  $\text{CaCO}_3$  relative to those in the IP and C (Manzello et al., 2017), and as the saturation state of aragonite is lower in the region, reefs show little evidence of submarine lithification when compared to the western Atlantic reefs (Manzello et al., 2008; Macintyre et al., 1993), and hence, are highly susceptible to the destructive forces of storms and wave action (Dana, 1975; Glynn and Ault, 2000). In the case that all the above mentioned environmental impediments for reef development in the ETP turn acute, the future of reefs in the region will not only depend on survival of branching or massive coral species, but on the ability of coral reefs to overcome a rapid changing environment as a complete ecosystem (reef metabolism); thus, ecosystem research might provide more accurate answers regarding the future of ETP reefs.

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## Conflict of interests

The authors declare that they have no conflicts of interest

## Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <https://doi.org/10.1016/j.ecolind.2018.08.021>.

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